



Long-term vegetation change in Scotland's native forests[☆]

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ABSTRACT

Forests play a key role in climate change mitigation, adaptation and delivery of a range of ecosystem services. There is increasing evidence for impacts of climate and other drivers on plant community change, and fragmented habitats are predicted to be much less resilient to negative impacts on biodiversity and other services. Within Europe, Scotland's native forests are highly fragmented and now cover 4% of the land after many centuries of degradation and loss, but little is known about how their species composition has changed. We recorded long-term vegetation change (from resurvey data) and examined the relationships with climate, pollutant deposition and grazing as key drivers of change, focusing on four forest types: pine, ash, acid- and base-rich oak-birch. All four forest types showed dynamic compositional change during 30–50 years between surveys, with increased species richness and decreased diversity. There was no evidence for homogenisation – the opposite was the case for all except pine (no change). Analyses indicate significant and varied climate, pollution and grazing impacts; NH₄ deposition showed the most frequent association with species compositional changes. Notable species changes include increases in pteridophytes and declines in forb cover, and a doubling in frequency and cover of *Fagus sylvatica* between surveys. Our findings suggest a possible extinction debt, with many more species declining than increasing between surveys. This trajectory of change and our other findings indicate a pressing need for mitigation management to reduce the risks of future species losses, with forest expansion planning explicitly considering spatial location in relation to existing native forest and those plant species identified as most at risk.

1. Introduction

Forests have a key role to play in climate change mitigation, adaptation and delivery of a wide range of ecosystem services, not least carbon sequestration (Millennium Ecosystem Assessment, 2005; Sing et al., 2018). They are subject to multiple pressures that impact on structure, function and composition and have suffered considerable degradation and loss in many parts of the world (Millennium Ecosystem Assessment, 2005; Curtis et al., 2018). Globally, net forest losses are still much greater than gains (Hansen et al., 2013; Curtis et al., 2018). Within the temperate/boreal zone, countries such as UK, Denmark and Netherlands have experienced significant fragmentation and loss of forest over many centuries (Rackham, 2001; Smout, 2003; Kaplan et al., 2009). In the UK, forest covers only 13% of the land area (1/3 of the European average (Quine et al., 2012)), of which c. 85% is plantation. A recent major national survey and mapping of native woodlands (Forestry Commission Scotland, 2014) found a high degree of fragmentation across all forest types. There is compelling evidence for

habitat fragmentation driving long-term ecological change (Opdam and Wascher, 2004; Haddad et al., 2015; Segan et al., 2016), with complex interactions with climate and other change-drivers (Opdam and Wascher, 2004; Gimona et al., 2015; Perring et al., 2018).

Pan-UK and pan-European analyses of long-term changes in temperate forests have emphasised the importance of multiple driver interactions and local site conditions (e.g. successional stage and soil nutrient status) in driving long-term changes (Kirby et al., 2005; Verheyen et al., 2012; Bernhardt-Römermann et al., 2015). Most UK and trans-national resurvey analyses to date have focused on lowland temperate forests (Kirby et al., 2005; Verheyen et al., 2012; Bernhardt-Römermann et al., 2015; Wood et al., 2015; Perring et al., 2018), but there are hypothesised to be major potential differences in responses of lowland versus upland forests, for example to climate change (Bertrand et al., 2011). In this paper we address this knowledge-gap by examining long-term compositional changes in Scottish native forests which include both upland and lowland temperate and boreal forest types. Using national datasets we examine impacts and interactions between climate

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variables, pollutant variables and herbivore numbers to establish the main drivers of change (herbivores can have transformative effects on forest composition, yet the latter have rarely been examined at national/trans-national levels due to a lack of data). Scotland experiences strong spatial gradients of both climate and pollutant deposition (RoTAP, 2012), with significant temporal changes recorded over the past 40+ years (Scottish Environment Protection Agency, 2006; Jenkins et al., 2008; RoTAP, 2012). Densities of the main large herbivore species also show strong spatial and temporal differences (e.g. SAC Rural Policy Centre, 2008; Albon et al., 2017).

The primary questions that we address are:

1. How has the species composition of Scotland's surviving native forests changed over the last 30–50 years, across all forest plots and within specific forest types?
2. What evidence is there for climate, pollution and/or grazing driving forest compositional changes over this period?

Note that we use the term 'forest' throughout this paper (amalgamating the terms 'forest' and 'woodland' which are often used interchangeably) for clarity of comparison with most global literature.

2. Materials and methods

2.1. Vegetation recording

Long-term vegetation changes in Scotland's native semi-natural forests were assessed by resurveying plant species composition of plots distributed across Scotland within different forest types. The original survey data comprised part of a large (6000 plot) dataset collected between 1958 and 1983 to describe the plant communities of Scotland (Birse and Robertson, 1976; Birse, 1980, 1984). A stratified random subset of the original 1240 forest plots was selected (to cover available geographic and altitudinal ranges). Each of these plots was then relocated (where possible – see below) and re-surveyed in 2007, and compositional changes were assessed by comparison with the original survey data.

For the original survey, homogeneous stands of vegetation considered representative of the plant community being described were selected and plant species composition recorded (Domin scale); ground vegetation was recorded within 2 m × 2 m plots, and tree (> 2 m height) species composition was mostly recorded within 100–200 m² plots (depending on heterogeneity and density of trees (see Birse and Robertson, 1976)). Plot records included grid-referenced location (± 50 m), altitude, slope, aspect, topographic information and any notable features. Plots were not permanently marked. Methods and plot sizes used for the resurvey followed those of the original survey, with the exception that all plant species cover estimates were recorded as percentages, rather than Domin values, to allow both compatibility with the original survey data and greater precision for future use. All plots were assigned to a National Vegetation Classification (NVC: Rodwell, 1991) community using Tablefit (Hill, 1996).

The resurveyed forest plots were widely distributed across geographical and altitudinal ranges (from 3 to 565 m a.s.l.) (Fig. A1). Plots were recorded at the same time of year as they were originally surveyed (to minimise seasonal variability) and survey methodology followed Britton et al. (2017). Relocation of plots followed a strict procedure: the original 100 m grid square was located using hand-held GPS; within this, the location for resurvey was then selected using the description of physical features on the original survey datasheet. Any plot not confidently relocated was not resurveyed. There is good evidence that this method of relocation is robust in detecting temporal vegetation change (Ross et al., 2010; Kopecký and Macek, 2015). As we were interested in change in species composition within surviving native forests (as opposed to change in forest coverage between the two surveys), any relocated plots that were no longer forested were excluded from our

resurvey. This gave a total of 263 forest plots resurveyed.

2.2. Data preparation

Before analysis, both datasets were checked for consistency of species nomenclature, and species not thought to have been recorded with equal rigour in both surveys were removed. Species that were difficult to separate with confidence in the field were amalgamated as appropriate. To standardise the two surveys, resurvey percent cover data were converted to Domin scores, then all original and resurvey data were transformed to percent cover using mid-points of the Domin categories. Broad forest types were defined based on floristic similarity using a Detrended Correspondence Analysis (DCA) with log-transformed species data from all forest plots in both surveys, detrended by segments, using 'decorana' in the 'R' package 'vegan' (Version 3.5.1 (2018), The R Foundation for statistical computing, Vienna, AT). The four forest types with sample sizes large enough for individual analysis were: *Ash* (comprising NVC W8, W9; Rodwell, 1991; $n = 37$), *Acid oak-birch* (NVC W17, W19; $n = 108$), *Base-rich oak-birch* (NVC W10, W11; $n = 54$) and *Pine* (NVC W18; $n = 36$). These forest types correspond to the following EC Habitats Directive Annex 1 Habitat codes: *Ash*: 9180; *Acid oak-birch* and *Base-rich oak-birch*: partial correspondence with 91A0; *Pine*: 91C0. Plot locations are shown in supplementary online Appendix, Fig. A1.

2.3. Analysis of vegetation metrics

For all forest plot data together and for each of the four individual forest types, the following analyses were carried out. Changes in species richness (total; major species groups) were analysed using Generalised Linear Mixed Models (GLMM) (Genstat v18) with a Poisson error term and log link function, with survey visit as fixed effect and plot ID as random (potential over-dispersion was accounted for in the models). Paired *t*-tests (Genstat v18) were used to compare mean cover-weighted Ellenberg scores (based on both higher plants and bryophytes) (Hill et al., 2004, 2007), Shannon Diversity (H), and percent cover of major species groups. All percent cover data were angular-transformed before analysis, except dwarf-shrub, pteridophyte and sapling cover which were $\log_{10}(+1)$ -transformed before analysis.

Species cover data were square-root transformed prior to calculation of a Bray-Curtis distance matrix. We then tested for significance of difference in overall species composition of the plots between surveys, for all plots combined and for each forest type, using permutational multivariate ANOVA using 'Adonis' in the 'R' package 'vegan' (R Foundation for statistical computing, Vienna, AT). Beta-diversity was calculated to assess the degree of variability in species composition between different plots at each survey date; comparisons between surveys indicate whether between-plot variability increased or decreased between surveys. The distance of plots to their habitat group centroid in the first and second survey was calculated using 'Betadisper' in the 'R' package 'vegan'. As Bray-Curtis dissimilarity is not Euclidean, distances were calculated from PCoA axes using the methods of Anderson (2006). Paired *t*-tests were used to test for a change in β -diversity between surveys.

Individual species cover changes (across all plots and within forest types) were analysed using paired *t*-tests, testing only those species present in at least 6 plots at first and/or second survey - for each species, only those plots where it was recorded as present at one or both surveys were included in the analysis. To reduce the chances of presenting false-positive results from multiple *t*-tests, only P values < 0.001 are used as indicators of a significant change in cover between surveys for all forest plots combined, and $P < 0.01$ for species changes within individual forest types.

2.4. Driver data

Vegetation change data were examined against a suite of drivers relating to climate (temperature, precipitation), pollutant deposition (nitrogen, sulphur) and large herbivore densities (sheep, cattle, red deer). For each parameter, mean values were calculated for the ten years immediately prior to individual plot survey dates, with the exception of the herbivore data as detailed below. Climate data were taken from the UKCP09 5 km resolution data from 1941 to 2011 (Perry and Hollis, 2005). To limit the number (and intercorrelation) of climate variables, we selected the following three parameters: winter (Dec–Feb) and summer (Jun–Aug) precipitation (mm); summer temperature (°C); (winter temperature was excluded as it was strongly correlated with summer temperature ($r^2 > 0.9$, $P < 0.001$)). Pollutant deposition rates (NO_x, NH_y, SO_x) for each plot in the 10 years prior to each survey date were calculated by combining the 5 km resolution CBED deposition surfaces of the UK for 2005 (Smith et al., 2000) with published historic scaling factors (Fowler et al., 2005). Estimated densities of cattle and sheep at 2 km resolution for 1969 onwards, based on Agricultural Census data, were obtained from the Edinburgh University Data Library (<http://Edina.ac.uk/agcensus>). This dataset was extended back to 1941 using published agricultural census data at the county level to interpolate data for each year based on the 2 km gridded distribution in 1969. Deer densities were calculated using red deer count data from 1961 onwards, interpolated into a spatial surface of annual density estimates, using data from Scottish Natural Heritage (SNH), Deer Commission for Scotland (DCS) and the UK National Biodiversity Network for areas not covered by DCS/SNH (see Albon et al., 2017). Estimates for plots sampled before the start of DCS recording in 1961 used the 1961 red deer density values, as red deer numbers were considered not to have changed greatly immediately prior to 1961 (Staines et al., 1995).

Changes in each environmental driver between first and second surveys were analysed for all plots combined using mixed models (fitted in Genstat v18), with the difference between the values corresponding to the two surveys as the response variable and the intercept as the only fixed effect. The year in which the first survey took place was fitted as a random effect and an isotropic power covariance structure was used for the residuals. Tests were performed using degrees of freedom that accounted for the fitted spatial covariance structure. Individual forest types were not analysed separately.

2.5. Vegetation – driver analyses

Relationships between change in vegetation parameters and environmental variables between first and second surveys were analysed using all-subsets regression (Genstat v18) as follows, with survey and plot ID always included in the model. Data for all three herbivore types were skewed and therefore log-transformed before analysis. Only those vegetation metrics that had changed significantly between surveys, plus Bray-Curtis dissimilarity between the two surveys, were analysed against drivers. For all species richness data, generalised linear models were used with a Poisson error term and log link function, and Plot ID as fixed effect. For percent cover, Ellenberg values, Shannon diversity and Bray Curtis dissimilarity, Linear Models were used. Analyses used ‘all possible models’ to select the combination of drivers that best explained the change in each vegetation metric, defined as models with the best combination of highest adjusted- R^2 and lowest Akaike Information (AIC) value, in which all parameters were significant at $P < 0.05$.

3. Results

3.1. Differences in vegetation metrics between surveys

Over the 30–50 years between surveys, there were statistically

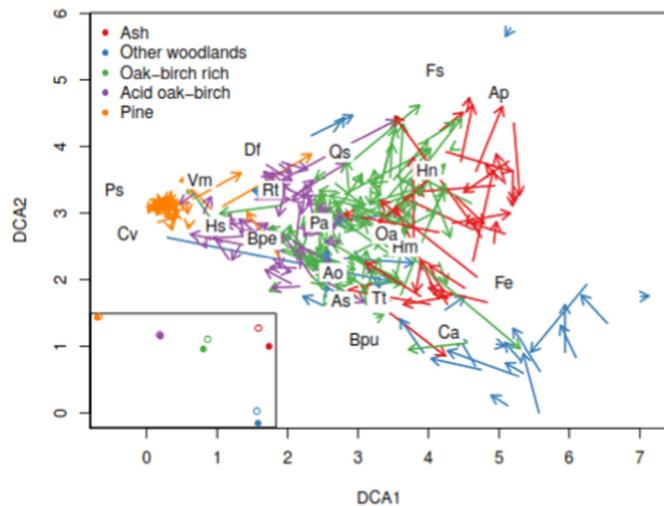


Fig. 1. DCA ordination of vegetation composition at first and second surveys, with each of the main woodland habitat types colour-coded as per the legend. The inset plot at the bottom LHS shows habitat centroid locations at first (filled-circles) and second (open-circles) surveys. Arrows n the main DCA plot show direction of change of all individual plots between first and second surveys. The positions of the 20 species with the greatest influence on the ordination are also shown: Ao - *Anthoxanthum odoratum*; Ap - *Acer pseudoplatanus*; As - *Agrostis spp*; Bpe - *Betula pendula*; Bpu - *Betula pubescens*; Ca - *Corylus avellana*; Cv - *Calluna vulgaris*; Df - *Deschampsia flexuosa*; Fe - *Fraxinus excelsior*; Fs - *Fagus sylvatica*; Hm - *Holcus mollis*; Hn - *Hyacinthoides non-scripta*; Hs - *Hylocomium splendens*; Oa - *Oxalis acetosella*; Pa - *Pteridium aquilinum*; Ps - *Pinus sylvestris*; Rt - *Rhytidodiplosis triquetus*; Qs - *Quercus spp*; Tt - *Thuidium tamariscinum*; Vm - *Vaccinium myrtillus*.

significant increases in β -diversity (i.e. compositional heterogeneity), across all forest plots combined and all individual forest types except pine (Fig. 1, Table 1). Pine forest showed the lowest β -diversity (least heterogeneity) amongst the forest types surveyed and this did not change significantly between surveys. The species composition change vectors on axes 1 and 2 of the DCA (Fig. 1) showed considerable variability in directions and magnitudes of change across individual plots, but the overall direction of compositional change was similar for all habitats except pine.

There were consistent, statistically significant declines in Shannon (H) diversity (Fig. 2a) between surveys for all forest plots combined and all individual forest types. Total species richness (Fig. 2a) increased significantly overall, driven by a highly significant increase in acid oak-birch.

Ellenberg L (light) values showed small but statistically significant increases between surveys, overall and in pine, acid oak-birch and ash (Fig. 2b). Only ash forest showed a statistically significant increase in Ellenberg N (nitrogen). Ellenberg R increased significantly in pine forest (indicating reduced acidity) and decreased significantly in ash. There were no statistically significant differences in Ellenberg F (moisture) values between surveys so this was not analysed further.

Tree species richness increased significantly in all forest types except ash, but canopy cover was similar at both survey dates (Fig. 3a). Tree saplings (< 2 m tall) were present in 66% of all plots at the first survey and 77% at the second, a trend consistent across all individual forest types (percentages of plots with saplings present changed between surveys as follows, for each forest type: pine 33–50% of plots; acid oak-birch 82–89%; base-rich oak-birch 70–78%; ash 73–89%). At both surveys, pine had the lowest proportion of plots containing saplings compared with all other forest types. Sapling species richness significantly increased between surveys, but total sapling cover per plot significantly decreased in all forest types except pine (Fig. 3b). Species richness and cover of dwarf shrubs showed no significant changes between surveys, but varied considerably between forest types (number of

Table 1

β -Diversity at first and second surveys, for all forest plots combined and for each forest type. S0 = first survey; S1 = second survey. Statistically significant changes (in bold): *** $P < 0.001$; ** $P < 0.01$; * $P < 0.05$.

All plots (n = 263)		Pine (n = 36)		Acid oak-birch (n = 54)		Base-rich oak-birch (n = 108)		Ash (n = 37)	
S0	S1	S0	S1	S0	S1	S0	S1	S0	S1
0.569	0.582 ↑***	0.272	0.291 ns	0.438	0.484 ↑***	0.500	0.542 ↑***	0.521	0.557 ↑*

species and cover were both greater in pine forests than any other forest types (Fig. 4a). Species richness of forbs did not change significantly between surveys in any forest types; but their cover declined significantly overall and in acid oak-birch, base-rich oak-birch and ash (Fig. 4b). Graminoid species richness increased significantly overall, but within forest types this was only statistically significant in acid oak-birch; their cover declined significantly in pine but increased significantly in ash forests (Fig. 4c). Pteridophytes showed no significant changes in species richness between surveys but significant increases in cover, both overall and in all forest types except pine (Fig. 4d). Bryophyte species richness and cover showed no significant changes between surveys (Fig. 4e). Shrubs and lichens were too infrequent to analyse statistically.

3.1.1. Individual species changes

Across all forest plots combined (Table 2), 21 species showed statistically significant changes in cover between surveys (one tree species, the others ground flora); of these, six showed significant ($P < 0.001$) increases, with *Luzula sylvatica* and *Fagus sylvatica* showing the largest increases, followed by *Pteridium aquilinum*, *Dryopteris dilatata*, *Dactylis glomerata* and *Ilex aquifolium* saplings. All these species also showed large increases in frequency of occurrence between surveys (particularly *Ilex*), with several doubling in frequency between surveys. Just over half the 15 species showing significant decreases in cover between surveys were forbs. Although most individual species cover-declines were small in absolute terms (only *Oxalis acetosella* showed a decline > 5% cover), given the low initial cover of many of these species,

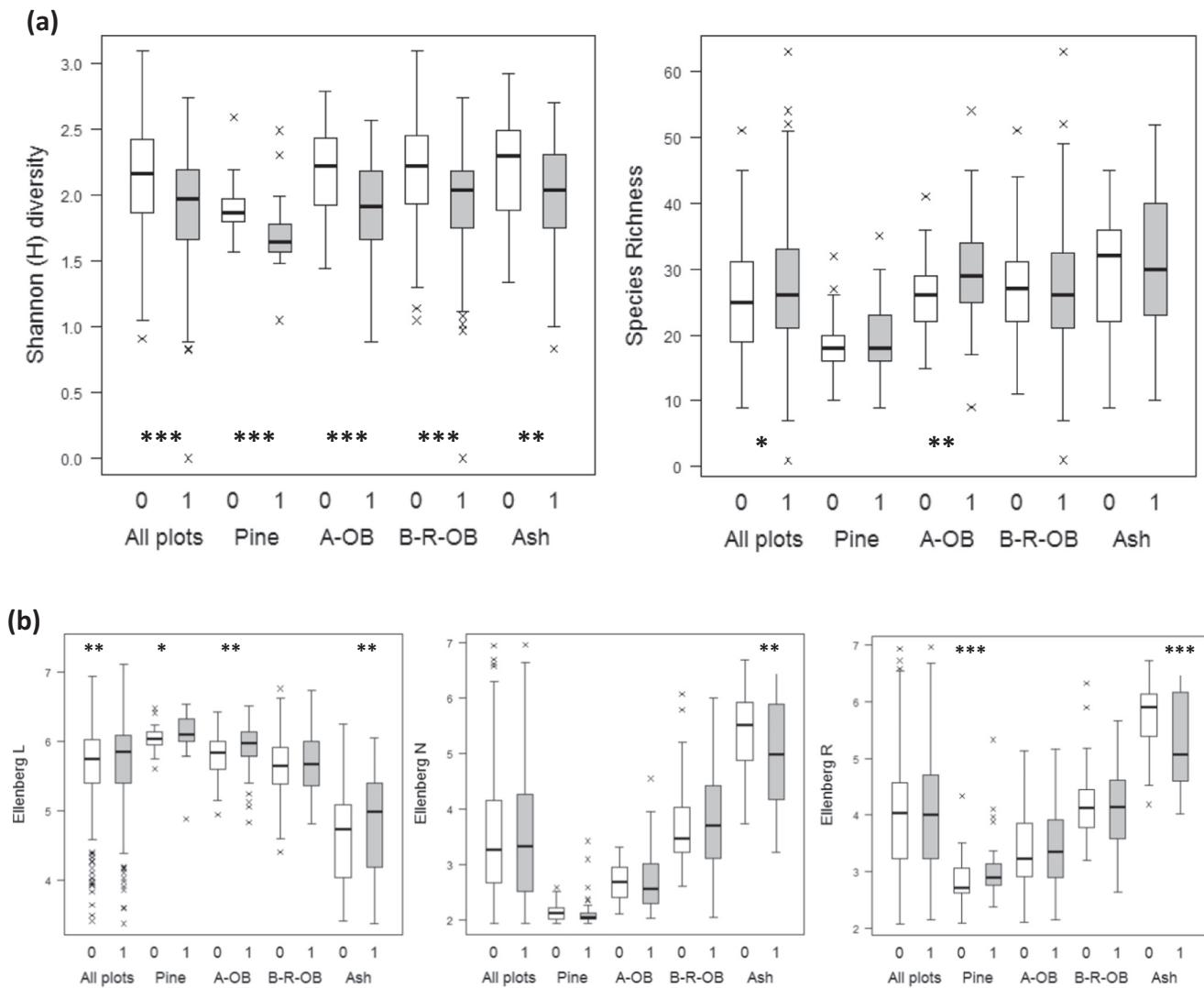


Fig. 2. Boxplots showing: (a) Shannon (H) diversity and species richness; (b) Ellenberg L, N and R, at first (0) and second (1 – shaded grey) surveys, for all forest plots combined ($n = 263$) and for each forest type. Sample sizes for each forest type are as follows: pine $n = 36$; acid oak-birch (A-OB) $n = 54$; base-rich oak-birch (B-R-OB) $n = 108$; ash $n = 37$. Statistically significant differences between surveys are shown as follows: *** $P < 0.001$; ** $P < 0.01$; * $P < 0.05$.

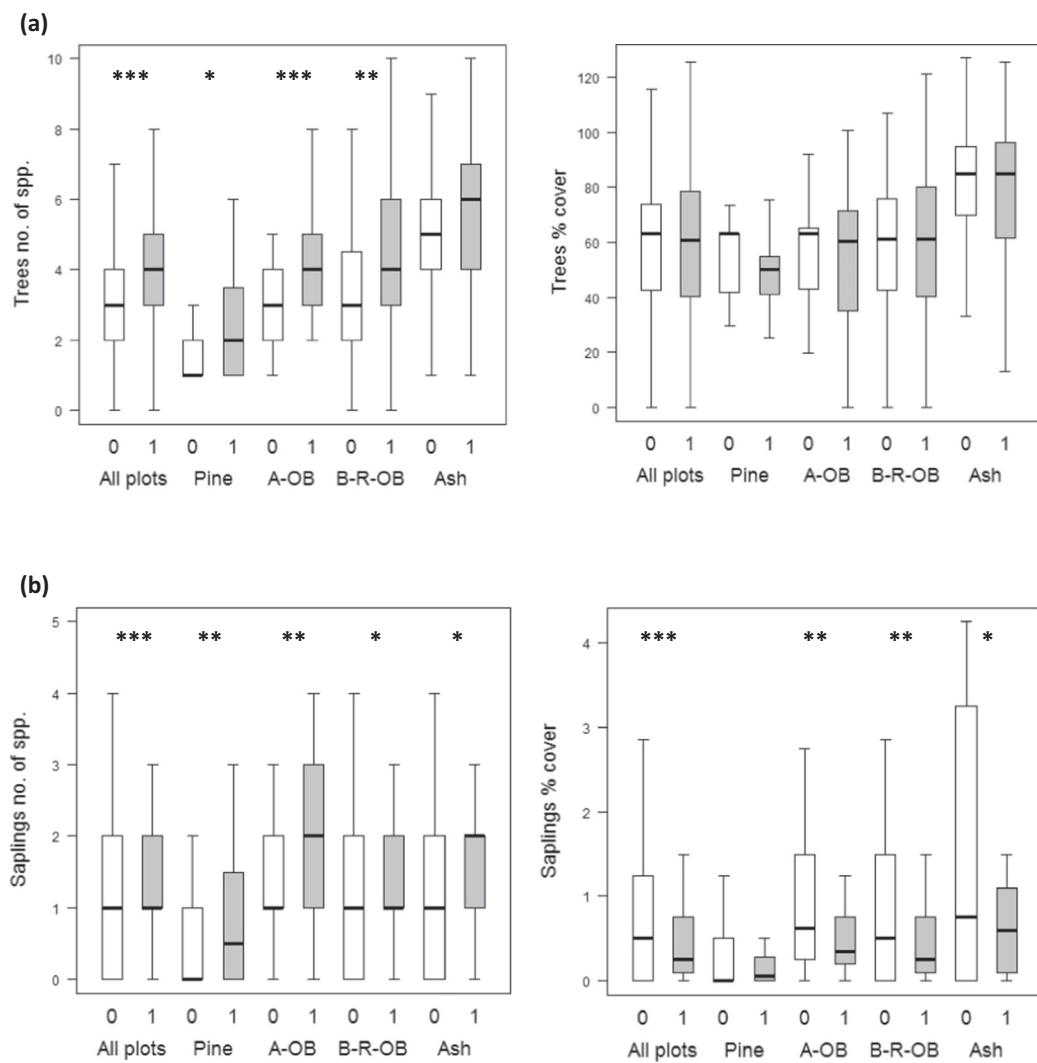


Fig. 3. Boxplots showing number of species and percentage cover of: (a) canopy trees; and (b) tree saplings (defined as < 2 m high), at first (0) and second (1 – shaded grey) surveys, for all forest plots combined ($n = 263$) and for each forest type. Sample sizes and codes as per Fig. 2. NB outliers are not shown on these boxplots to allow bigger scaling of y-axes for visual comparison of medians and interquartile ranges.

in proportional terms most changes were very large. Almost all significant changes in cover of individual bryophyte species were negative.

Within individual forest types there were also many fewer species with statistically significant ($P < 0.01$) increases in cover as compared to decreases (Table A1). In pine forest, all except one significant species changes were negative, with only *Hylocomium splendens* showing a significant increase in cover between surveys. In acid oak-birch *Pteridium aquilinum* showed a large, significant increase in cover. *Ilex* and *Quercus* saplings both showed small absolute but large proportional increases in cover and more than fourfold increases in frequency between surveys. All 9 other significant species cover changes in this habitat type were declines. In base-rich oak, only 4 out of 22 species showing statistically significant changes in cover had increased: *Pteridium aquilinum*, *Dryopteris dilatata*, *Dactylis glomerata* and *Hedera helix*; all others had declined in cover between surveys. The species with the biggest significant cover decrease between surveys was *Oxalis acetosella* (but its frequency did not decline). In ash forest plots, 4 out of 8 species showing statistically significant changes had increased in cover: *Corylus avellana* saplings, *Deschampsia flexuosa*, *Dicranum scoparium* and *Polytrichastrum formosum* (all also showing major increases in frequency between surveys). Species that had declined significantly were *Oxalis acetosella*, *Potentilla sterilis*, *Brachypodium sylvaticum* and *Erythronium striatum*.

3.2. Changes in drivers between surveys

For all forest plots combined, all drivers except sheep density changed significantly between surveys (summer temperature, winter rain, NH₄, NO_x, SO_x: $P < 0.001$; summer rain, cattle, red deer: $P < 0.05$. Table 3). Summer and winter precipitation and summer temperatures all increased (following national trends), as did NH₄ deposition, cattle and deer densities; SO_x and NO_x deposition declined between surveys. Individual forest types (summary data in Table A2) were not tested for statistical significance as sample sizes in some habitats were too small to allow fitting of a spatial covariance structure. Herbivore densities varied greatly between different forest types: cattle and sheep were recorded as most numerous in the locality of ash and base-rich oak birch, and deer in the locality of acid oak-birch plots (Table A2).

3.3. Vegetation change – driver relationships

Across all forest plots, species compositional change (Bray-Curtis dissimilarity) was positively associated with increasing summer rain, NH₄ and SO_x (Table 4). Pine forest plots were the most compositionally similar between surveys, with Bray-Curtis values negatively associated with increasing summer temperatures and positively associated with

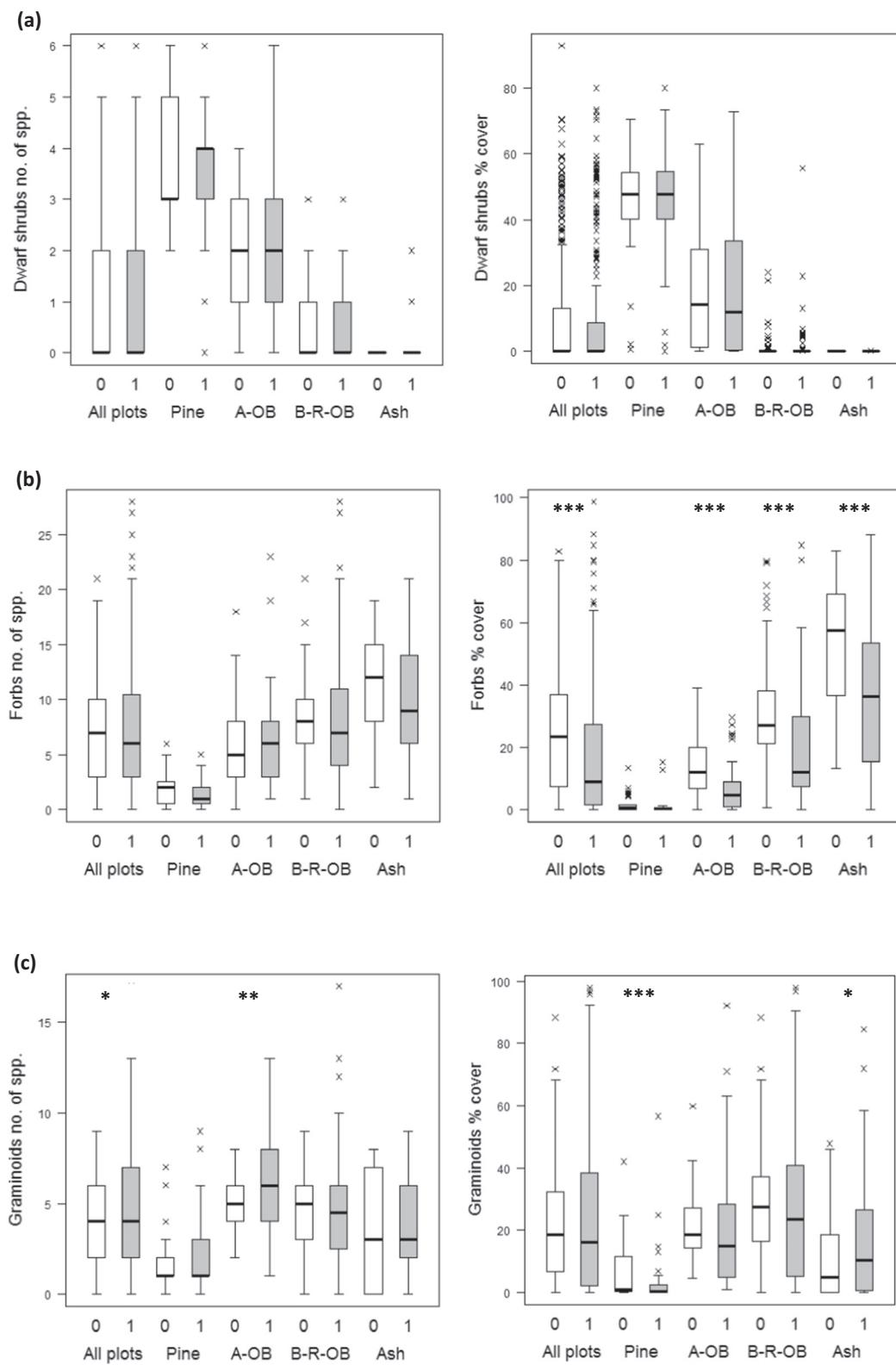


Fig. 4. Boxplots showing number of species and percentage cover for: (a) dwarf-shrubs; (b) forbs; (c) graminoids; (d) pteridophytes; (e) bryophytes, at first (0) and second (1 – shaded grey) surveys, for all forest plots combined ($n = 263$) and for each forest type. Sample sizes and codes as per Fig. 2.

higher numbers of cattle. Declining Shannon diversity across all forest plots was primarily associated with increases in NH_y, but also increases in cattle and sheep numbers. Within individual forest types, declining Shannon H in acid oak-birch was associated with fewer deer; in base-rich oak-birch with lower levels of NH_y but higher cattle numbers; and

in ash forest plots with increasing summer temperature, winter rain and higher numbers of sheep. Species richness increase across all plots combined was positively associated with summer rain and NO_x and negatively associated with winter rain, NH_y and SO_x. Species richness change in acid oak-birch was also positively associated with summer

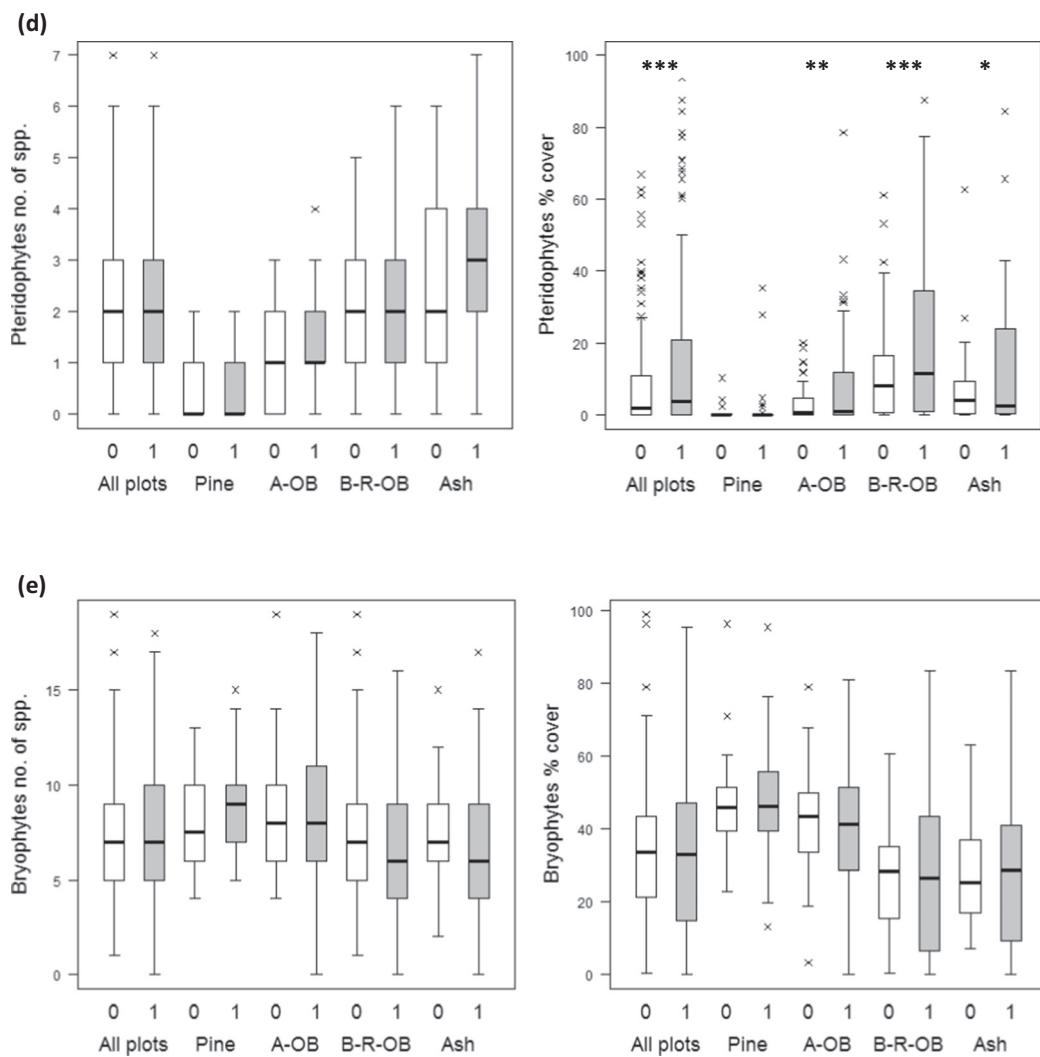


Fig. 4. (continued)

rain but negatively associated with sheep numbers. Across all forest plots, the increase in Ellenberg L between surveys was associated with decreasing SOx (Table 4). Within individual habitats, increased Ellenberg L in pine plots was positively associated with winter rain and sheep, in acid oak-birch negatively associated with NH₄, and in ash negatively associated with summer temperature and sheep. The Ellenberg R increase in pine plots was positively associated with NH₄ and SOx and negatively associated with summer temperature.

The decline in cover of forbs (Table 4) was associated with increases in SOx (overall and in acid oak-birch) and sheep (overall and in base-rich oak-birch). In base-rich oak-birch the decline in forbs was also associated with increasing summer rain. Over all woodland plots combined, there were no significant associations between graminoid cover and drivers, but within forest types the decline in graminoid cover in pine plots was associated with lower sheep numbers, and the increase in graminoids in ash plots was negatively associated with winter rain. Increasing pteridophyte cover was positively associated with NH₄ overall, in pine and in ash plots. In pine, increasing pteridophyte cover was also positively associated with winter rain and NOx; in ash it was also negatively associated with cattle; in base-rich oak-birch it was positively associated with summer temperature. The statistically significant changes in mean number of tree species (across several forest types) were not significantly associated with any drivers. The overall increase in mean number of graminoid species was negatively associated with summer temperature and SOx.

4. Discussion

All the forest habitats surveyed showed evidence of dynamic compositional change during the 30–50 years between surveys, with increased species richness and decreased Shannon diversity, reflecting the multiple individual changes in species cover and frequency, the most notable of which are discussed below. Significant compositional changes were also found in ancient temperate forests across 23 regions of Europe over similar timescales (Verheyen et al., 2012), but those forests showed much local variation with no consistent overall changes in species richness or diversity. There was no evidence for homogenisation across any Scottish forest types, in fact the opposite was the case for all forest types except pine (which showed no significant change). In all habitats except pine, the general shift between surveys towards greater dominance of pteridophytes (especially *Pteridium aquilinum* and *Dryopteris dilatata*) and declining cover of forbs concurs with several other studies (Corney et al., 2008; Verheyen et al., 2012) and gives cause for concern if dominant species such as *Pteridium* continue to increase in cover, as is predicted with climate warming in the UK (see Pakeman and Marrs, 1996). Our findings of increased overall species richness over the 30–50 years between surveys are consistent with several national (Britton et al., 2017; Mitchell et al., 2017; Pakeman et al., 2017) and pan-European studies of non-forest habitats (e.g. Steinbauer et al., 2018: mountain summits). Other studies of long-term change in temperate forests have produced divergent

Table 2

Mean cover and frequency (number of plots occupied) of species recorded in 6 or more plots that changed cover significantly between surveys (at $P < 0.001$) across all forest plots ($n = 263$). For each species, only those plots where it was recorded as present at one or both surveys were included in the analysis ($n = \text{number of plots}$). PG = plant group (T = trees; G = graminoids; F = forbs; P = pteridophytes; B = bryophytes). Sap = sapling. S0 = first survey; S1 = second survey; Ch = change; t = t-statistic.

Species	PG	n	Mean % cover			Frequency			
			S0	S1	Ch	t	S0	S1	
<i>Luzula sylvatica</i>	G	38	1.5	22.8	21.3	4.01	21	33	12
<i>Fagus sylvatica</i>	T	27	16.5	29	12.5	4.46	11	26	15
<i>Pteridium aquilinum</i>	P	169	5.9	13.9	8.0	5.62	128	146	18
<i>Dryopteris dilatata</i>	P	79	5.1	10.2	5.2	4.5	49	69	20
<i>Dactylis glomerata</i>	G	32	0.4	3.4	3.0	3.67	14	26	12
<i>Ilex aquifolium</i> Sap	T	24	0	0.2	0.2	5.95	3	23	20
<i>Luzula pilosa</i>	G	99	0.9	0.3	-0.7	-5.88	81	63	-18
<i>Mnium hornum</i>	B	96	1.1	0.2	-0.9	-4.37	69	49	-20
<i>Sorbus aucuparia</i> Sap	T	144	1.2	0.3	-0.9	-4.02	99	110	11
<i>Campanula rotundifolia</i>	F	34	1.2	0.2	-1.0	-3.67	28	16	-12
<i>Dicranum scoparium</i>	B	129	1.2	0.2	-1.0	-3.49	86	95	9
<i>Potentilla erecta</i>	F	139	2.4	1.1	-1.3	-4.52	116	118	2
<i>Trientalis europaea</i>	F	51	1.8	0.4	-1.3	-5.07	47	30	-17
<i>Galium saxatile</i>	F	148	1.9	0.4	-1.4	-7.58	126	107	-19
<i>Viola riviniana</i>	F	164	2.6	1.3	-1.4	-4.89	133	133	0
<i>Anemone nemorosa</i>	F	102	3.7	1.5	-2.3	-4.76	75	74	-1
<i>Betula pubescens</i> Sap	T	81	2.7	0.3	-2.4	-3.89	55	40	-15
<i>Pleurosticum schreberi</i>	B	140	3.6	1.2	-2.4	-5.88	118	102	-16
<i>Melampyrum pratense</i>	F	59	3	0.3	-2.7	-5.2	46	40	-6
<i>Eurhynchium striatum</i>	B	52	6.1	2.7	-3.4	-3.66	46	20	-26
<i>Oxalis acetosella</i>	F	193	7.8	2.7	-5.1	-8.58	169	166	-3

Table 3

Environmental driver values at first and second surveys, for all forest plots combined ($n = 263$). Mean values (=10 year means prior to each survey date – see Materials and methods). Statistically significant changes are indicated in bold: *** $P < 0.001$; ** $P < 0.01$; * $P < 0.05$.

Driver	First survey	Second survey
Summer temp (°C)	10.6 ± 0.1	11.5 ± 0.1 ↑***
Summer rain (mm)	528 ± 11	551 ± 11 ↑*
Winter rain (mm)	672 ± 20	827 ± 24 ↑***
NH ₄ (kg·ha ⁻¹)	8 ± 0.2	10 ± 0.3 ↑***
NO _x (kg·ha ⁻¹)	12 ± 0.2	9 ± 0.2 ↓***
SO ₂ (kg·ha ⁻¹)	19 ± 0.4	8 ± 0.2 ↓***
Cattle (no·km ⁻²)	14 ± 1.0	18 ± 1.3 ↑*
Deer (no·km ⁻²)	5 ± 0.5	6 ± 0.5 ↑*
Sheep (no·km ⁻²)	69 ± 5.2	67 ± 5.1 ns

findings, including declines, no change, and increases in species richness over time (e.g. Bernhardt-Römermann et al., 2015; Kirby et al., 2005; Reczyńska and Świerkosz, 2017).

Our finding of multidirectional associations between species changes and different climate and pollutant variables is in line with other long-term studies of forest systems (Kirby et al., 2005; Verheyen et al., 2012; Bernhardt-Römermann et al., 2015; Perring et al., 2018). Forests are generally more structurally complex than many open ground habitats and we propose that one primary reason for the high variability in findings from long-term studies of forest species composition relates to differences in successional stage and, in particular, differences in light levels reaching the forest floor, which can have strong interactive effects with other drivers (Kirby et al., 2005; Bernhardt-Römermann et al., 2015; Landuyt et al., 2018). This also highlights the importance of forest management legacy in driving structural, as well as compositional change (Perring et al., 2018).

4.1. Tree canopy composition

The main contributor to the small, but significant increase in mean number of canopy tree species was *Fagus sylvatica*, which more than doubled in frequency and cover between surveys. This may reflect a positive response to increasing temperatures in this northern part of its range (Falk and Hempelmann, 2013; Cheddadi et al., 2016) and/or continuing postglacial expansion (Magri, 2008). The contrast between the dynamic sapling and ground-flora species compositional changes and the relative stability of canopy species composition illustrates an important point: focusing on tree canopy composition alone can give an impression of forest stability which can mask other significant changes, e.g. within the ground-flora. Furthermore, canopy ‘stability’ can also mask a climatic debt (particularly relevant for slow-growing species), where changes in climatic suitability reduce the likelihood of ongoing recruitment of the same canopy species. Both have important implications, for example in using protected forests as ecological ‘reference-points’ e.g. for restoration or conservation management decisions (Josefsson et al., 2009; Huntley et al., 2018). Huntley et al. (2018) provide simulation results suggesting that Caledonian pine might be one such forest type where, as a result of changes in climatic conditions over the past 200+ years, the ‘most favourable’ areas for pine growth are now outside the current ‘core’ Caledonian pine forest where most conservation action is focused.

4.2. Changes in overall species composition – evidence for an extinction debt?

The preponderance of species showing significant declines in cover (and frequency) between surveys as compared to species showing significant increases could be evidence of an extinction debt (Kuussaari et al., 2009; Cousins and Vanhoenacker, 2011; González-Varo et al., 2015). If this pattern of change continues (particularly under further climate change) then we could predict major reductions in species richness (particularly forbs) across all the forest types studied. Haddad et al. (2015) presented strong evidence for time-lagged species responses to fragmentation within forest systems, including species extinctions, giving support not just for extinction debt, but also the linked processes of immigration lag and ecosystem function debt. Given that Scotland’s remaining native forest covers only 4% of Scotland’s land area and the remaining forest patches are highly fragmented (see Forestry Commission Scotland, 2014 maps; Gimona et al., 2012), they are undoubtedly vulnerable to local extinctions and increases in more common, generalist species (as we found). The possibility for species migration between the remaining forest patches (e.g. under further climate change) will be very limited, particularly for forest specialist species (Ford et al., 2009; Bertrand et al., 2011; Hodgson et al., 2012; González-Varo et al., 2015), many of which have limited dispersal ability (Gimona et al., 2015).

4.3. Pollutant deposition as a driver of change

We found evidence for pollutant-related vegetation changes (primarily for NH₄), almost always in association with other drivers. An exception to this was the positive relationship between increases in pteridophytes and NH₄ deposition (cf Verheyen et al., 2012). Bernhardt-Römermann et al. (2015) found greatest diversity changes in areas with lowest accumulated N at first survey, which our findings would also support. In contrast to Smart et al. (2003), we found no evidence for eutrophication (as indicated by Ellenberg N values) in any of our upland forest habitats, probably reflecting the lower N deposition levels over much of Scotland in comparison to the rest of UK and parts of Europe (RoTAP, 2012). Our results for ash forests indicate a shift towards more acidic, lower nutrient conditions (Ellenberg R and N) between surveys for this forest type. Changes in Ellenberg R scores have been negatively linked to acid deposition (SO_x and NO_x) (Rose et al.,

Table 4

Significant regression models using (a) Multiple Linear Regression and (b) Generalised Linear Models of vegetation metrics against drivers, at first and second surveys. Only those vegetation metrics that changed significantly between surveys were analysed (see Table 2), as well as Bray-Curtis mean dissimilarity between first and second surveys (values given in brackets below). The direction of the relationship (positive/negative) is denoted by + or -. Significance levels: *** $P < 0.001$; ** $P < 0.01$; * $P < 0.05$. ns: no statistically significant driver relationships found. Blank cells indicate that the vegetation metric did not change significantly between surveys and was not analysed.

Vegetation metrics	All plots (n = 263)	Pine (n = 36)	Acid oak-birch (n = 54)	Base-rich oak-birch (n = 108)	Ash (n = 37)
(a):					
Bray-Curtis dissimilarity (value in brackets)	+ RainS*** + NHy*** + SOx* (0.481)	– TempS** + Cattle*** ns	ns	ns	ns
Shannon (H) diversity	– NHy*** – Cattle* – Sheep** – SOx***	(0.295)	(0.462) + Deer**	(0.531) + NHy*** – Cattle*	(0.556) – TempS* – RainW* – Sheep* – TempS* – Sheep*
Ellenberg L		+ RainW*** + Sheep**	– NHy*		ns
Ellenberg N Ellenberg R		– TempS** + NHy** + SOx*			ns
Forb cover	– SOx* – Sheep**		– RainS* – SOx*	– Sheep***	
Graminoid cover		+ Sheep**			– RainW*
Pteridophyte cover	+ NHy**	+ RainW*** + NHy*** + NOx*	ns	+ TempS**	+ NHy** – Cattle**
(b):					
Species richness	+ RainS*** – RainW*** – NHy*** + NOx*** – SOx***		+ RainS** – Sheep*		
No of tree species	ns	ns	ns	ns	
No of graminoid species	– TempS*** – SOx*		ns		

2016), but the fundamental relationships between, for example light- and nutrient-limitation give additional complexity in untangling their interactive effects in forest systems (cf. Kirby et al., 2005; Bernhardt-Römermann et al., 2015; Stevens et al., 2016). It has been suggested, for example, that dense forest canopies (i.e. reduced light levels) might buffer the effects of enhanced N availability (Kirby et al., 2005; Verheyen et al., 2012). Although we found no significant overall relationship between pollutant deposition and total bryophyte cover/ frequency, we suggest that the large number of individual bryophyte species showing declines (particularly in pine) might reflect negative impacts of the ongoing increases in NHy deposition (Phoenix et al., 2012; Reinecke et al., 2014), as reported from several different ecosystems across the major bioclimatic zones in Europe (Dise et al., 2011).

4.4. Herbivore impacts and interactions with other drivers

The transformative (and interactive) impacts of herbivores on vegetation have been extensively demonstrated (e.g. Gill, 2006; Hester et al., 2006) - Speed et al. (2012), for example, showed good evidence at individual site level for the capacity of herbivore impacts to effectively reverse predicted processes of climate-driven change in treeline vegetation. But spatial datasets of herbivore population densities are uncommon, making national (or wider) analyses of their impacts highly challenging. Analyses of herbivore impacts in long-term forest plot studies (Kirby et al., 2005; Verheyen et al., 2012; Bernhardt-Römermann et al., 2015) have generally used local estimates of herbivore use or indicators such as proportions of grazed shoots. UK native forests have a long history (many centuries) of open access to both wild and domestic herbivores. But as far as we are aware, this is the first time that national level datasets of herbivore densities have been used alongside climate and pollutant deposition datasets to analyse and demonstrate their relative contributions to long-term vegetation change.

In this respect it is important to note that free-ranging herbivores are highly mobile, and these national datasets only give an indication of herbivore use at any specific location (e.g. Albon et al., 2007, 2017).

Within our 30–50 year time period, the associations between increases in cattle and deer numbers and declining plant species diversity were in line with expectations (e.g. Vild et al., 2017). Tree regeneration can be suppressed by herbivore browsing (Gill, 2006) and the more than sevenfold increase in mean frequency of *Ilex aquifolium* saplings between the two surveys (concurring with Kirby et al., 2005) indicates a window of reduced grazing between the two survey dates, as this species is readily browsed (e.g. Conedera et al., 2017). While our analysis included herbivore density estimates from the two ten-year windows prior to each survey date, this masks considerable fluctuations in sheep densities across Scotland within the intervening period - broadly, increases in sheep numbers until 1980–90 were followed by widespread declines (SAC Rural Policy Centre, 2008; Britton et al., 2017). The observed increase in tree sapling frequency between surveys could have occurred in direct response to the recent declines in numbers of sheep.

4.5. Implications for the future of Scotland's native forest resource

Our finding of increased compositional heterogeneity between surveys may reflect the lack of connectivity between many remaining forest areas (Forestry Commission Scotland, 2014). Our findings also highlight the potential threat of major future species losses (extinction debt) in these highly fragmented forest habitats; and understanding the associated main drivers gives an opportunity for better-targeted restoration action to prevent or reduce species losses (González-Varo et al., 2015; Auffret et al., 2018). Within the Scottish Biodiversity Strategy (Scottish Government, 2013) there are specified targets for forest expansion and a strong focus on improvement of connectivity,

reflecting the ‘Aichi Biodiversity Targets’ in the Convention on Biological Diversity’s Strategic Plan for Biodiversity 2011–2020. In countries such as the UK with such a small remaining native forest resource, the targets for expansion to address national and international targets and priorities have broad stakeholder support in terms of potential public benefits (e.g. Burton et al., 2018). However, any habitat expansion necessarily results in reductions in other land-cover types, and informed spatial targeting and management is critical (Gimona et al., 2012, 2015; Huntley et al., 2018; Isaac et al., 2018; Sing et al., 2018), as well as appropriately prioritised financing mechanisms (Hermoso et al., 2017). For example, the degree to which improvement of forest networks might help species range shifts (e.g. under climate change) is strongly dependent on dispersal ability, but also on speed of dispersal in relation to speed of change in, for example, a specific climate driver (Gimona et al., 2015). For slow dispersers under rapid climate change, the most viable option might actually be translocations. Understanding the medium and longer-term change trajectories for different species (as in this paper) is a critical first step in defining and prioritising species-related conservation action. Relating these to different measures of connectivity within the landscape (e.g. Hodgson et al., 2012), including identifying potential time-lags in species responses to habitat configurational change (e.g. Lindborg and Eriksson, 2004; Bertrand et al., 2011), are important, though challenging, next steps (Isaac et al., 2018).

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.biocon.2019.04.018>.

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